FASCIATION

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(WITH SEVEN FIGURES)

During the spring of 1910, while an examination of a tree claim near Larimore, North Dakota, was being made, there were discovered some pronounced cases of fasciation. The tree claim had been planted to cottonwoods and willows in 1885. During the winter of 1909 the owner had taken considerable fuel from the northern portion of this grove of vigorous trees. In the summer of 1909 a large number of sprouts came from the stumps of the

FIG. 1.—A portion of the original timber claim and three years' growth of the cut-over region adjoining.

trees which had been removed (fig. 1). The number of sprouts was variable on different stumps, but in all cases the growth was pronounced and occasionally it was extreme, some of the sprouts having reached a height of two or three meters. On all of the stumps of the cottonwoods and on some of those of the willows one or more fasciated sprouts appeared. The flattening was particularly marked near the outer extremities of the stem, and was accompanied generally by profuse branching and forking of the fasciated specimens. The most superficial markings on the

fasciated sprouts were prominent cortex ridges along the whole axis of the young plant. Fig. 2 shows the relative size and the shape of the cortex ridges and also the flattened xylem and pith in a transverse section of modified cottonwood stem. This section

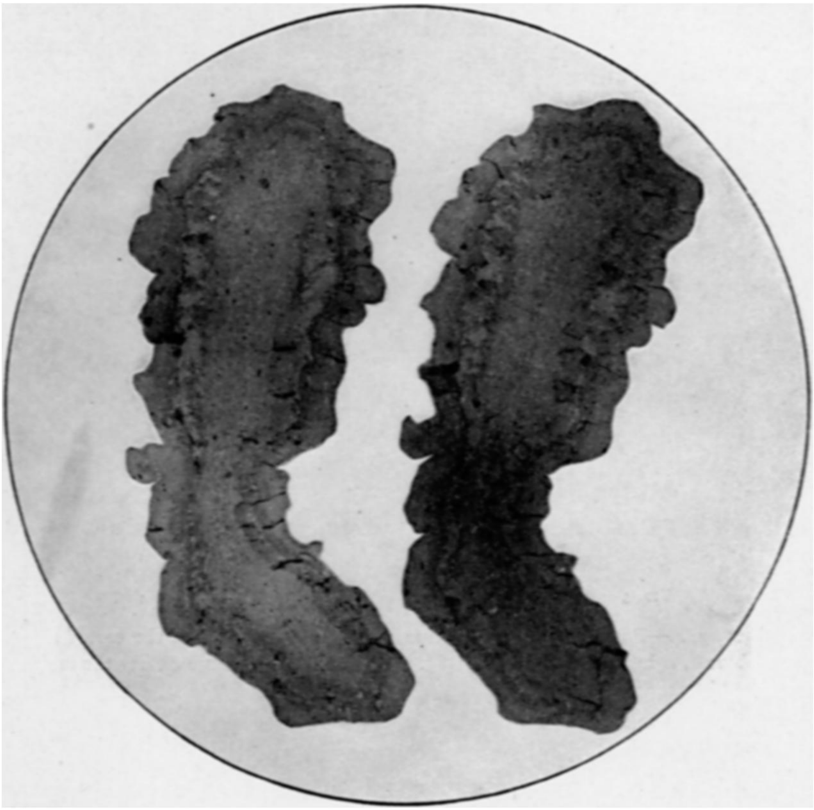

FIG. 2.—Transverse section of a fasciated cottonwood stem one year old; ×8; the notable cortex ridges and change of symmetry in the cross-section of the stem are well illustrated by these sections.

shows that pith, xylem, phloem, and cortex maintain the same relative positions in the abnormal specimens that they have in the normal cottonwood stem. The two exaggerated features of these flattened stems are the huge cortex ridges and the modification of radial symmetry.

The phenomenon of fasciation is not rare among plants, though it is not often reported for those having woody stems. Manifestly, the disturbing features, whatever they may be, which produced "banding" or "bundling" must have been considerably more pronounced in the wooded stems of cottonwoods, ash, willow, and other woody plants than they are in herbaceous stems of seedlings of pumpkin, young stems of thistles, floral axes of coxcomb, stems of asparagus, and other fasciated herbs.

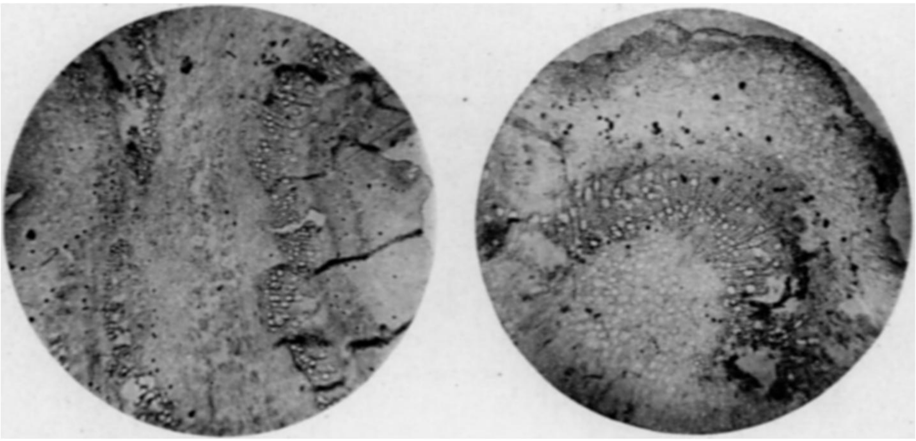

FIG. 3 FIG. 4

FIGS. 3, 4.—Parts of the stem section showing the relation of the cortex ridges with phloem, xylem, and pith; ×13; fig. 4, section showing more clearly the relation indicated in fig. 3; ×25.

The number of atmospheres of pressure requisite for the flattening of a wooded stem corresponding to the cottonwood shown in the accompanying section (figs. 3 and 4) has not been determined. It is evident, however, that an enormous molecular disturbance would be required in order to change the molecular arrangement which caused the disturbance of radial symmetry of these woody stems. In seeking for the cause of the energy release which was expressed by this modification of symmetry, one naturally inquires into the chemical and physical factors involved. With reference to the chemical factors it seems evident that the stumps of the cut-away trees did not contain other compounds than those which

had been moving freely through the tissues of the tree while it was standing. There might have been larger quantities of various chemical substances per unit of living tissue, but hardly a different quality than that present in the uncut cottonwoods and willows. The soil had not been disturbed; there had been no change in drainage, and no great variation of precipitation during the latter months when the trees were standing and during the time that the fasciated sprouts had been developed. This seemed to indicate that, so far as the causes of fasciation in the stems of cottonwood and willow were concerned, it was necessary to seek them among physical rather than among chemical factors. From the list of physical factors such as light, gravity, and turgor it was easily possible to select turgor as the one which would be variable in the meristematic tissue near the exposed surface of the tree stumps out of which numerous sprouts developed. Root pressure of the cottonwood and willow plants was apparently in full operation during the early spring months after the trees had been cut away. The full flow of sap was directed into the meristematic tissues of the stumps from which a few buds developed in the early spring. This seemed the probable cause in the production of the phenomenon of cottonwood and willow fasciation.

Traumatism may have been involved in the changes registered in the young, rapidly growing sprouts. However, this seemed improbable, inasmuch as numerous sprouts were wholly free from fasciation, notwithstanding the fact that some of the more pronouncedly fasciated sprouts came from the same stumps on which normal sprouts were growing. Transition from the abnormally fasciated to the normal radial symmetry was evidenced by the most strongly fasciated sprouts after three seasons of growth. Figs. 5 and 6 show the bases of cottonwood saplings which had sprouted from the stumps four years before. The wide scar near the base of each fasciated specimen clearly indicated the location of a ruptured cortex which took place in the deeply furrowed fasciated specimen during its second season's growth. The dimensions of the cross-section of the base of the specimen shown in fig. 5 were 6 by 4.5 cm. Fig. 6 shows the base of a fasciated stem whose cross-section 15 cm. from the ground was 6.5 by 5 cm.

Fig. 7 shows a stem whose cross-section 25 cm. from the ground was 11×9.5 cm. These variations in symmetry were gradually

FIG. 5

FIG. 6

FIG. 7

FIGS. 5–7.—Basal lateral views of the sprouts three years after the beginning of fasciation, illustrating separation of cortex from woody cylinder and consequent exposure of wood to weather.

lost, and practically disappeared in fasciating sprouts at the end of three years' growth. Nearly all of the specimens which had such manifest banding and bundling during their first three years

of growth had changed to symmetrical cylinders having practically no evidences of fasciation beyond the terminal portion of the third season's growth. The uniform diameter in all parts of the stem produced during the fourth year, together with its smooth, firm bark, presented a great contrast to the unsymmetrical, fluted cortex produced during the three previous seasons. Seemingly the distribution of stress and the physical and chemical factors had reached stages similar to those which prevail in the production of normal cylindrical stems.

HUS[1] states that fasciation may be produced experimentally in annuals (*Phaseolus multiflorus* and *Vicia Faba*). The stems of these annuals fasciated when they were cut off directly above the cotyledons, and the roots fasciated when the tips were amputated or split. HUS also showed in work carried on at the Missouri Botanical Garden that plants with an indeterminate inflorescence would fasciate when treated as follows:

> About the time of the appearance of the first flowers the plant is kept as dry as possible, only enough water being given to prevent wilting. As a result, the flowering period will be comparatively short, and, in an indeterminate inflorescence, the buds near the end of the spike remain undeveloped. If at that time the plants are daily abundantly irrigated, occasionally with manure water, numerous fasciations will make their appearance, but it must be remembered that this result is usually reached only with plants which throughout their existence have been well nourished and well cared for generally. For no apparent reason, one plant will fasciate, while the next one belonging to the same species remains normal.

From this and other experiments, HUS concludes that GOEBEL is correct when he affirms that fasciation results from the rapid introduction of sap into stems which would not normally have fasciated. This conclusion was further supported by experiments carried on at Berkeley, California, in September 1904. Within a week after a heavy rainfall a very large number of teratological cases appeared. They were represented by fasciations, by torsions of the stem, petalody of the stamens, phyllody of the pistils, and prolongations of the axis through the center of the flower, known as frondiferous diaphysis. HUS further cites the experiences of

[1] Mo. Bot. Gard. Report, 1906, pp. 147–152.

some asparagus growers in California, who testified that there was a greater percentage of fasciated shoots in their beds of asparagus during the period when the first stems pierce the soil, especially after a cold winter.

DEVRIES conducted experiments[2] in his garden at Amsterdam, and minutely studied fasciated plants in their natural conditions. From the experiments and observations he agrees heartily with GOEBEL that fasciation is due to internal stimuli, notably increasing pressure of cell sap.

The whole question of monstrosities might be ignored but for the light their study throws upon numerous morphological structures among plants. To illustrate some of these morphological problems the lists of floral parts which are closely united have been cited. In the whorl of microsporophylls one often finds a complete union of the filaments, also the fusion of megasporophylls in the formation of compound ovaries; the fusion of the petals in the gamopetalous corolla, as for instance in the orchids; the fusion of seed coats in cycads; the fusion of nucellus and integuments in some of the other gymnosperms; the fusion of the bract with the axillary flowering stock in basswood (*Tilia americana*); and the union of the calyx with the ovary as in the apple and other pomaceous fruits. This group of morphological modifications was classified as negative by WORSDELL.[3] The same author classifies as positive congenital increase of parts the following: the pappus or the sepals in the Compositae; twin embryos which develop from a single egg that divides vertically perhaps instead of transversely; and twin flowers which arise by the modifications of the apical region of growth.

WORSDELL holds that, in addition to these congenital fusion problems, there are those which may be called post-genital; for example, the plantain with twin spikes of flowers at the summit of the stem, the *Campanula* with four flowers borne at the apex of an abnormal stem, the leaves of the *Oxalis* sometimes individual instead of being in three parts as is customary, the fusion of the flowers in *Crocus*, and lastly fasciation itself. In support of his view that the various monstrosities in plants are sometimes con-

[2] Die Mutationtheorie 2:541. 1903.

[3] New Phytol. 4:55–74. 1905.

genital and sometimes post-genital, he has recourse to a theory of CHURCH, who holds that "growth is distributed at the apex of a shoot in such a manner that its transverse component may be expressed by a plane, circular construction around a circular point (the growth center), and the circular section of the vast majority of plant axes is evidently the outcome of such a regular and symmetrical distribution from the growing point." WORSDELL approves of CHURCH's theory that central distribution is distributed around several points instead of about one center of growth. He holds that some growth centers are weaker than others, hence develop less in diameter and elongate more slowly, and this produces torsion, which is an almost invariable component of fasciation. Having developed this theory of centers of growth in different radii of the apical region of a stem, he holds that any force which upsets the equilibrium of the organism will tend to bring about a reversal to ancestral conditions. In other words, cylindrical woods like those of our cottonwood and ash, upon losing their balance, will repeat the long-past experience of lycopods, ferns, and algae, where branching primarily is probably in one plane.

WORSDELL furthermore treats of plant monstrosities as a possible pathological condition. He refers to it as a subtle diseased condition brought about by superabundant nutrition that destroys the balance of the organism and produces hypertrophy of parts. It is pointed out that the crested form of *Celosia argentea* is not produced abundantly without manuring the potted plants. WORSDELL'S conclusion is that there are morphogenetic principles underlying the phenomenon of fasciation. He holds that fasciation is to be explained as a resultant of the more or less equal conflict waged between two opposing tendencies or forces, one of which induces integrity of parts of a plant and the other induces plurality of parts.

In a recent discussion, WHITE[4] reviews interesting genetic studies based upon a fasciated variety of *Nicotiana Tabacum*. The race of these fasciated specimens was obtained from the self-fed seed of a mutant found growing in a field of Cuban tobacco. He

[4] WHITE, O. E., The bearing of teratological development in *Nicotiana* on theories of heredity. Amer. Nat. **47**:216–228. 1913.

suggests that these studies indicate that "the gene for fasciation appears to me to lie deeper in sporogenesis than the chromosome." "The abnormal character development appears most easily interpreted from a physiological standpoint." Whether or not his contention is correct that "physiological" factors rather than chromosomes control the continuous fasciation through the chain of alternation of generations, there can be no question, however, regarding the fact that some physiological factor, notably sap pressure, is intimately associated with the control of the fasciation of ash, willow, and cottonwood on stems found on tree stumps in the North Dakota tree claim.

The examples of fasciation presented in this paper have been noted because of the bearing which the study of abnormal structures may have upon the study of normal morphological structures; and also because of the possible interesting physiological relation existing between increased sap pressure and the disturbed balance of forces which are believed to be responsible for cottonwoods and willows undergoing a change from radial to more or less bilateral symmetry of stem during their first three seasons of growth.

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